# GROWTH GRADIENTS AMONG FOSSIL MONOTREMES AND MARSUPIALS

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ABSTRACT. Although a few groups appear to be characterized by relative stability of size, growth gradients, whether isometric or allometric, have played an important role in the evolution of Australian monotremes and marsupials.

Intra-specific size reduction, resulting from isometric change, has been a widespread phenomenon from Pleistocene to Recent. Its implications were not recognized by early taxonomists, whose undue emphasis on minor size differences as a criterion of speciation, and even failure to compare fossil and recent forms, have led to nomenclatorial confusion in some families. Further study of the available fossil and recent material in such groups suggests cases of conspecificity, and the consequent priority of either a palaeospecific or neospecific name.

In certain marsupials such as the Diprotodontids and the wombats, there is evidence of a trans-specific increase in size, involving allometric as well as isometric changes, and leading to gigantism and subsequent extinction. Evidence of the progressive stages by which such gigantism was achieved in the Diprododontinae is given, and a new genus and species of this subfamily of the Diprotodontidae is described.

GROWTH gradients, whether isometric or allometric, may be evidenced in phylogeny as well as in ontogeny. In the phylogeny of mammals this phenomenon has long been recognized, and a progressive phyletic increase in body size is known to have occurred at some stage in the ancestry of most eutherian orders. Similarly, the earliest fossil marsupials are relatively small types, and gigantism, which reached its peak in the Pleistocene, was not apparent at first. Such samples of progressively increasing body size in lines of descent are commonly referred to under *Cope's Rule* and are numerous.

On the other hand, there are few quoted cases of a graded trans-specific decrease of body size. The rarity of such broad-scale dwarfism gives a false impression of the role size reduction has played in mammalian evolution. Although on a lesser scale, and at an intra-specific level, the phenomenon of size reduction is very much in evidence when one compares Pleistocene and Recent mammals. As Hooijer (1951) has stated, it is fairly common to find Pleistocene animals, in all parts of the globe, both on continents and islands, larger than the living individuals belonging to the same species. No extinction nor even migration is involved; it is evolution *in situ*. The means and modes of the various metrical characters are shifting in the course of time, thus producing temporal clines or chronoclines.

The quaternary decrease in the intraspecific size of many mammals is little understood. The size decrease is quite appreciable, and may be as much as 20–25 per cent. Such isometric changes occurring within one and the same species produce many problems in the equating of fossil and recent forms and in the sorting out of geographical and temporal races. Whatever the factor or factors involved, palaeontologists giving first descriptions of certain Australian fossils last century and in the first half of this century understood little, if anything, of this phenomenon. They commonly ascribed to distinct species fossil forms which merely exhibited slight size differences, but which were otherwise morphologically indistinguishable from living forms at the specific level. Any systematic study of the present-day Australian monotremes and marsupials should

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therefore take due cognizance of the validity of various fossil species that have been described. If growth gradients are isometric, conspecificity may be recognized and taxonomic revision may be required.

In view of these problems, the following account of selected monotremes and marsupials is provided and suggestions concerning their generic and specific nomenclature are made. Failure in the past to equate fossil and recent species, when this would have been possible merely by using the available data, has in itself left a legacy of taxonomic problems. Article 1, International Code (1961), makes it quite clear that zoological nomenclature is the system of scientific names applied to taxonomic units of animals known to occur in nature, whether living or extinct.

This study is based on a comparison of both fossil and recent material in the British Museum (Natural History) and in various Australian museums and university departments. In some instances, material is reidentified, and in one case a description is given of a new genus and species.

## SIZE CRITERION IN TAXONOMY

The taxonomic confusion which may arise, even at the generic level, when size is used as a criterion, is exemplified by certain monotreme species of the family Tachyglossidae.

The genus *Tachyglossus* was first designated in 1811 by Illiger. This is the oldest generic name available for the spiny anteater of the Australian mainland, Tasmania, and New Guinea, because Cuvier's (1798) *Echidna*, which is preserved in the vernacular, was preoccupied by Forster (1788) for a genus of eels within the family Muraenidae (Echidnidae).

By the end of 1876 *Tachyglossus* was the valid generic name not only for mainland and Tasmanian species of the spiny anteater, but also for a new species from New Guinea, which Peters and Doria had described in that year under the name of *Tachyglossus bruijnii.* This generic name should also have been applied by Krefft when he described the first fossil species in 1868. Krefft's material, the proximal end of a humerus, was scanty and was described under the name *Echidna owenii.* In 1884 Owen examined the cast of a more perfect example of a humerus, which he described under the name *Echidna ramsayi*, but which is now regarded as being identical with Krefft's species. This first fossil species, of which more material has subsequently been found, is still more correctly known as *Tachyglossus owenii* (Krefft, 1868).

In 1877 Gill, in referring to the newly described New Guinea form, wrote: 'This has very lately (December 3, 1876) been described by Messrs. W. Peters and G. Doria as a new species of the genus *Tachyglossus*, under the name *T. bruijnii.* It nevertheless differs markedly from the *T. hystrix* (= *T. aculeatus*) and *T. setosus* of Australia in the much more elongated and nearly uniformly or very gradually attenuated and decurved rostrum, as well as in the contour of the palate, etc. So great are these differences that . . . the newly discovered form may therefore be appropriately contrasted under the name *Zaglossus bruijnii*, with the previously known *Tachyglossus hystrix* and *Tachyglossus setosus.*'

Although these relatively minor morphological differences of rostrum curvature and palate contour might well have been questioned as hardly constituting generic distinctiveness, Gill's proposal of a separate generic name for the large New Guinea species has been generally accepted by subsequent writers. For example, Laurie and Hill (1954) list, apart from *Tachyglossus lawesii* Ramsay, which occurs in south-east New Guinea, three species of the genus *Zaglossus* Gill. These are *Z. bruijnii* (Peters and Doria), *Z. bartoni* (Thomas), and *Z. bubuensis* Laurie, and various subspecies.

Whether, in 1877, Gill was aware of a fossil species, then already described, which was even larger than this largest of living species with which he was concerned, is not known. In proposing a new generic name, he made no attempt to accommodate the fossil species. Apart from large size, in which it exceeded *Z. bruijnii*, other diagnostic features of generic significance to Gill were, and still are, unknown in *T. owenii*. Because of its size, however, this fossil form probably had a proportionally long beak with which to reach the ground.

Whatever the justification of Gill's description of the species *bruijnii* under the new generic name of *Zaglossus*, which in any case had priority over *Acanthoglossus* (= *Proechidna*) suggested by Gervais (November 1877), there seems to be little validity in the reference of later fossil species, in none of which are details of rostrum and palate sufficiently well known, if at all, to any genus other than *Tachyglossus* (Illiger, 1811).

Dun (1895) described an imperfect skull and atlas vertebra of a fossil species from Gulgong, New South Wales, under the name *Echidna* (*Proechidna*) *robusta*. He claimed that this species was much larger and more robust than the living forms, and also than *T. Owenii*. Dun further stated that these vertebral and cranial remains seemed to show a greater resemblance to *Proechidna* than *Echidna*, although he commented on the uncertainty of Oldfield Thomas (1888) as to the distinction of these two genera. It is clear that Dun was very uncertain as to how this new fossil species should be generically designated. On the evidence available, Dun's species should more correctly be referred to as *Tachyglossus robustus* (Dun).

Further confusion in the fossil nomenclature was caused in 1914 when Glaubert described a fossil species from material collected at the Mammoth Cave, one of a series of limestone caverns in Western Australia. Glaubert's material consisted of an atlas vertebra, clavicles and episternum, pelvic girdle, two femora, a tibia and a radius, and was referred by him to a new species, *Zaglossus* (*Proechidna*) *hacketti*. Again, no adequate reason was given for assigning this species to a genus other than *Tachyglossus*, and the criterion of size was inadequate. The other minor differences in limb bones and girdles observed by Glaubert appear merely to mark distinction at the sub-specific or specific level.

One important feature which distinguishes the large New Guinea anteater from other living species, including *Tachyglossus lawesii* Ramsay, from Port Moresby, is the reduced condition of its digits. There are normally only three claws on each limb, but the reduced first and fifth digits, both before and behind, are represented in the skeleton by phalanges and, according to Oldfield Thomas (1888), in some cases by functionally developed claws. However variable in extent it may be, this reduction of first and fifth digits of fore and hind limbs in the so-called three-toed anteater, *Zaglossus*, seems a more satisfactory basis for generic or subgeneric distinction amongst living forms, if such is desired, than any other feature so far proposed. Nevertheless, it was a character not commented upon by Gill (1877) in his original claim of generic status for *Zaglossus bruijnii*. There is, furthermore, no information as to whether digital reduction is solely a recent trend characteristic of the New Guinea species, or whether it had already been embarked upon by any of the fossil species. Under these circumstances it seems preferable at present to sustain the fossil forms as species of the genus *Tachyglossus*.

## PRIORITY OF A PALAEOSPECIFIC NAME

In 1838 Richard Owen described a fossil marsupial from the Wellington Caves, New South Wales, under the name of *Dasyurus laniarius*. He stated that it resembled the Tasmanian Devil, a species now confined to Tasmania, but that it differed in being one-third larger, and in having the canines, or laniaries, of proportionately larger size. At this stage, no other criterion than that of size was used.

By 1877 Owen (pp. 105–6) was recognizing his fossil species as belonging to the genus *Sarcophilus* Cuvier and Geoffroy Saint-Hilaire, 1837. Some of the material from the Wellington Caves he assigned to the same species as the existing Tasmanian form, but other specimens from the same locality he included in his fossil species, *Sarcophilus laniarius* (Owen, 1838). With regard to these latter specimens, he stated that: ‘Besides the difference in size, the following modifications of structure are noticeable. The larger and deeper digital pit on the inner or palatal side of the penultimate upper molar; the better and broader ossification of the medial border of the palatal vacuity. In the under jaw the relatively broader and deeper symphysis; the wider interval between the two predental foramina, and the more backward position of the hinder one, beneath the fore part of the antepenultimate molar.’

Lydekker (1887) did not question the validity of Owen’s defined fossil species. He stated that *Sarcophilus laniarius* ‘presents a considerable excess in size’ over the existing Tasmanian form, ‘but may probably be regarded merely as the ancestral form of the latter, which, from inhabiting a continental area, attained superior dimensions’. Lydekker further suggested that the smaller specimens from the Wellington Caves, assigned by Owen to the same species as the existing form, were probably females of the fossil species.

Lydekker’s measurements for *Sarcophilus laniarius* have been checked, e.g., 5·6 cm. for the length of the check-teeth series in specimen B.M. Cat. No. 42555; 3·95 cm. for the length of space occupied by the three teeth in specimen B.M. Cat. No. 42559. The corresponding measurements of a male specimen of the recent Tasmanian species are 4·9 cm. and 3·6 cm. respectively. Such comparative measurements do not support Lydekker’s contention of a fossil species presenting ‘a considerable excess in size’ over the existing Tasmanian form.

A comparison of recent and fossil specimens in the collections of the British Museum, including Owen’s type material, suggests that there is insufficient evidence for the recognition of a fossil species as distinct from the existing form. In nomenclatorial revision, the palaeospecific name, *Sarcophilus laniarius* (Owen, 1838) would take precedence over *S. harrisii* (Boitard, 1841) if, as seems to be the case, *S. ursinus* (Harris, 1808) is already invalidated as a name for the living Tasmanian Devil.

Certain corrections to the legends of original illustrations should perhaps be noted here. In Plate 31, accompanying Owen’s letter which is published in Mitchell’s (1838) *Three Expeditions into the Interior of Eastern Australia*, Fig. 6 is described as the ‘left ramus, lower jaw, with last grinders’, and Fig. 7 as ‘anterior part of the right ramus of lower jaw’. Both are ascribed to *Sarcophilus laniarius*, although Owen expresses doubt, because of the spacing of teeth, as to whether the specimen illustrated in Fig. 7 is really the lower jaw of *S. laniarius*, or of some extinct marsupial carnivore of an allied but distinct species. By 1845 Owen had seen a specimen of *Thylacinus spelaeus*, and consequently revised his identification of the anterior portion of the right lower jaw, illustrated in Fig. 7, Plate 31 (1838). This is now ascribed to a fossil species of *Thylacinus*, namely *T. spelaeus*. Owen's correction may be carried further to include the specimen illustrated in Fig. 6 of the same plate. This is also a portion of the lower jaw of Owen's *T. spelaeus*, namely, a part of the left mandibular ramus, viewed from the outer side, and illustrating the last tooth in the jaw. Probably the portions of the left and right lower jaws, illustrated in Figs. 6 and 7, both belong to the same animal.

In Fig. 2, Plate 32, Owen illustrates the smaller bones in the foot of a *Dasyurus*, by which name *Sarcophilus* was at that time known to him. These small bones have now been cleared of matrix and some of them have been reassembled. These include what are undoubtedly the second, third, fourth, and fifth right metacarpals, the proximal phalanx of the fourth digit, and a carpal bone. The bones are clearly those of a small wombat.

## PRIORITY OF A NEOSPECIFIC NAME

The Thylacine of Australia, commonly known as the Tasmanian or Marsupial Wolf, or Tiger, was first described by Harris (1808) under the name of *Didelphis cynocephala*. The generic name *Thylacinus* was established by Temminck (1827) and the Thylacine, which recently has been restricted to Tasmania, and which may already be extinct there, is known as *Thylacinus cynocephalus* (Harris).

Despite the restriction of the living Thylacine to Tasmania, fossil material of this genus has been recorded from various localities on the Australian mainland. Owen (1845) distinguished fossil material under a new specific name, *Thylacinus spelaeus*. In 1877 Owen (*Extinct Mammals of Australia*, p. 106) used the name *T. major* for the first time. According to Lydekker (1887), this name was given inadvertently for *T. spelaeus*; the mandible represented in Pl. V, Fig. 8, being drawn from the last three molars of *Sarcophilus laniarius* added to the hinder part of a mandible of *T. cynocephalus*.

Owen distinguished *T. spelaeus* on the following criteria: in one specimen (No. 1548, Cat. Royal College of Surgeons, 1845), the depth of the lower jaw below the first premolar was nine-twelfths of an inch, whereas that of the corresponding part of the jaw in the existing Thylacine was seven-twelfths of an inch; in another specimen (No. 1549, Cat. Royal College of Surgeons, 1845), the penultimate molar of the right side of the lower jaw had a small accessory cusp on the inner side of the large middle compressed cusp; an upper canine, erroneously described in 1877 as *T. major*, was proportionately larger in comparison with the lower one than it is in *T. cynocephalus*.

Such slight differences and size distinctions of individual specimens used by Owen appear to be too inadequate as a basis for full specific recognition. Under these circumstances, it seems best to recognize only one species of *Thylacinus*, namely, the neospecies *T. cynocephalus* (Harris).

## SIZE STABILITY IN PHYLOGENY

In 1900 Baldwin Spencer described *Wynyardia bassiana*, a fossil marsupial from marine sediments near Wynyard, northern Tasmania. This was the first and for many years the only reputedly Tertiary marsupial from Australasia, and is still the oldest Tertiary marsupial of more precisely known age from this region (Woods, 1962).

In the complete absence of teeth and of bones of the feet of this fossil, Spencer was led to the conclusion that it was representative of a new extinct series of forms which were more nearly allied to ancestral Polyprotodonts than are any of the existing Diprotodont forms. He regarded *Wynyardia* as intermediate between the former and the latter, and as indicative of a stage in the development of Australian marsupials when the ancestors of recent Diprotodontia were beginning to diverge from their original Polyprotodontid stock.

In 1930 Wood Jones re-examined *Wynyardia* and, in reviewing the skull, observed that there were singularly few noteworthy characters to differentiate it from that of a modern phalanger. In general outline, the proportions of the skull preserved in the specimen resembled very strikingly the similar parts of a rather large skull of the Tasmanian form of the phalanger, *Trichosurus vulpeculus*. From his re-examination of parts of the postcranial skeleton, Wood Jones deduced that *Wynyardia* was a sturdily built creature, considerably heavier than the living *Trichosurus*, and probably differing from that animal in habit and in bodily poise. His illustrations, however, show only slight differences, and, on the whole, the evidence points to relatively little change from the Tertiary to Recent, involving a size decrease so slight as to be possibly within the limits of subspecificity. Certainly, there is no evidence of phylogenetic gigantism in this or any other form that is comparably arboreal. Stirton (1957) described a new genus and species, *Perikoala palankarinnica*, possibly Oligocene, from the Palankarinna fauna, east of Lake Eyre, South Australia. This early phascolarctine is of roughly comparable size to the modern *Phascolarctos* and to *Trichosurus*. Again, in this ancestry, there is evidence only of size stability.

Owen (1838, p. 361) described a fossil phalanger from the Wellington Caves, but recognized that a comparison with the bones of *Trichosurus vulpeculus*, known to him as *Phalanagista vulpina*, but not available in his osteological collections, would be necessary to establish whether or not his fossil material was specifically different from the modern form. Owen's original material is available for examination at the British Museum (Natural History) and appears to be specifically identical with recent skulls of *T. vulpeculus*.

Gill (1957) concluded that *Wynyardia bassiana* is a valid fossil, having the same age as the *Turritella* bed in which it was found, and with a fluorine index of nearly 500 times as great as that of *Trichosurus vulpeculus* living in the same area in modern times. The issue of the inclusion of *Wynyardia* in the Phalangeridae seems settled. Rather the main question today is whether its generic distinction from *Trichosurus* is really justified. With one incomplete fossil skeleton in which only part of the skull is represented, and that completely lacking teeth, this question remains unanswered.

## GRADIENTS LEADING TO GIGANTISM IN THE DIPROTODONTINAE

Richard Owen (1838) gave the first description of *Diprotodon optatus*, which fossil species is now known as the largest Australian marsupial. Subsequently, three further species, *Diprotodon minor* Huxley, 1862, *D. longiceps* McCoy, 1876, and *D. bennetti* Owen, 1877 were described, although Owen (1877) himself expressed the view that

*D. minor* was founded on teeth of a species of *Nototherium*. Whatever the validity of these species of *Diprotodon*, they certainly indicate forms which were smaller, but at the same time reasonably close to *D. optatus* in size. De Vis (1888) commented on the fact that *D. minor* was but a fourth smaller than *D. optatus*, and from the measurements given by McCoy (1876) and Owen (1877) *D. longiceps* and *D. bennetti* were apparently not less than this.

No precise information has been available regarding the progressive stages whereby gigantism could have been achieved in the Diprotodontinae, nor has irrefutable evidence existed of gradients leading to *Diprotodon optatus* from very much smaller forms. With the exception of the nothothere *Meniscolophus mawsoni* Stirton, 1955, the fragmentary remains of smaller diprotodontids so far found have not been referred beyond the subfamilial level. None appear to have been ascribed to the subfamily Diprotodontinae. Owen (1877, p. 274) stressed the fact that the first incisors of *Diprotodon* were scalpriform, ever-growing tusks, with enamel continued to the widely open bases. On the other hand, the incisors of *Nototherium* were teeth of limited growth, each with a well-defined, partly enamelled crown, and a non-enamelled root. The incisors are therefore very important in enabling a diprotodontine to be distinguished from a nothothere.

There is now evidence that gigantism has been progressive in the Diprotodontinae. Stephenson has given evidence (in press) to support the view that the scalpriform upper incisors known as *Sceparnodon ramsayi* actually belong to a small member of the Diprotodontinae, and that they were erroneously restored on to the front part of a skull of *Phascolonus gigas* by Stirling (1913). An even smaller diprotodontine was found at Wellington Caves by Mr. J. Mahoney, University of Sydney, in 1954. This specimen consists of part of the left premaxilla with the complete first and second incisors implanted, and also part of the alveolus of the third incisor of the left side (Plate 90, figs. 1 and 4). This fragment is indicative of a diprotodontine related to *Diprotodon*, and belonged to an animal which appears to be the smallest of the series yet to be discovered. In contrast to *Diprotodon optatus*, which in bulk fully equalled a large rhinoceros, this animal would have been about the size of a Shetland pony.

The first incisor is strongly curved and increases in width from its tip to base. The length of the tooth is approximately 5 inches, but of this only about 1 inch would project beyond the alveolus. The enamel of this incisor is continued to the base of the tooth and bears the same relationships to the dentine as in other diprotodontine teeth. The worn surface at the tip bears a transverse notch which no doubt was caused by the lower incisor.

The second incisor is the small, typically peg-like tooth found in such a position in other diprotodontids, but it is proportionately larger than the corresponding tooth in *Diprotodon*. It is well worn, but remarkable in exhibiting on the inner and outer sides of its crown small patches of enamel. This enamel does not extend back to the root, and is limited to the sides of the crown. In possessing enamel, this tooth resembles those of nototheres in which enamel appears normally to be present on the crowns of the second and third upper incisors. There is no previously recorded case of enamel occurring on the diprotodontine second and third incisors which, as in nototheres, are also teeth of limited growth. In describing a specimen of *Diprotodon optatus*, Owen (1877, p. 199) stated that probably, by reason of the age of the individual, and the extent of tooth worn away, the original enamelled crown had gone, and both $I_2$ and $I_3$ were represented only by their cylindrical cement-covered portion. However, there is no evidence from the specimens in the Australian Museum that enamel is ever developed on the second and third upper incisors of *Diprotodon.*

The reidentification of *Sceparnodon ramsayi* Owen as a member of the *Diprotodon* series makes it desirable that this more recently discovered diprotodontine, which is even further removed from *Diprotodon* than is *Sceparnodon*, should be ascribed to a new genus and species. The type specimen is not unique. Gill (1955) appears to have erroneously ascribed a portion of an identical incisor (Plate 90, fig. 2) to the very much larger diprotodontine, *Diprotodon minor* Huxley. This specimen, described by Gill, is a right upper incisor and is a very much worn tooth. In the Queensland Museum there is a left upper incisor, F.1651, which is only slightly worn. There are also two casts of an identical upper incisor, L.1292 and F.5056 (Plate 90, fig. 3), in the Australian Museum collection, although there is no trace of the original which had been in an old collection in Sydney.

## SYSTEMATIC DESCRIPTION

### Genus DIARCODON gen. nov.

*Type species. Diarcodon parvus* sp. nov.

The diagnostic characters of the genus are those of the genotypic species until other species have been described.

### *Diarcodon parvus* sp. nov.

Plate 90, figs. 1–4

*Holotype.* Left premaxilla, with first and second upper incisors implanted and entire. Australian Museum Collection, Reg. No. F.50099.

*Paratype.* Portion of a well-worn, right upper incisor. National Museum of Victoria, Reg. No. P.16155.

*Diagnosis.* First upper incisor small, flattened, arcuate; tapering slightly from root towards tip, though more markedly so beyond the alveolus; dorsal outline slightly concave; root open; enamel extending back to root, covering dorsal and part of lateral surfaces. Second upper incisor peg-like, with enamel on crown; small, but strongly developed and proportionately larger in relation to first upper incisor than in *Diprotodon.*

*Description.* Total length of $I_1$, 120 mm.; greatest width, at root, 30 mm.; depth varying from 15 mm. near root to 10 mm. near tip; length of tooth normally exposed beyond

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EXPLANATION OF PLATE 90

Fig. 1. *Diarcodon parvus*, gen. et sp. nov. Lateral view of holotype showing first upper incisor, second incisor with patch of enamel, and part of alveolus of third incisor. Australian Museum Collection, Reg. No. F.50099. ×1·2.

Fig. 2A, B. First upper incisor (right) of *Diarcodon parvus.* Paratype, Nat. Mus. Vict. Reg. No. P.16155. A, Dorsal view; B, mesial view. ×0·6.

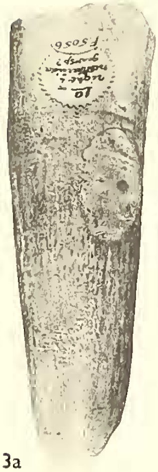
Fig. 3A, B. First upper incisor (left) of *Diarcodon parvus.* Cast, A.M. Reg. No. F.5056. A, Dorsal view; B, mesial view. ×0·6.

Fig. 4A, B. Upper incisors of *Diarcodon parvus.* Holotype, A.M. Reg. No. 50099. A, Dorsal view, first upper incisor; B, as in Fig. 1, but mesial view. ×0·6.

1

2a

2b



3a

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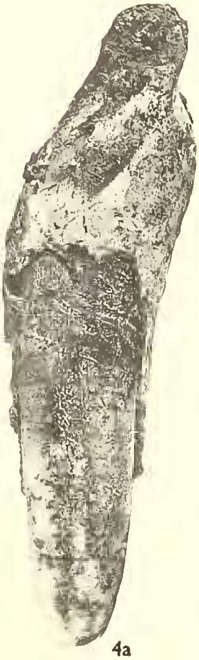
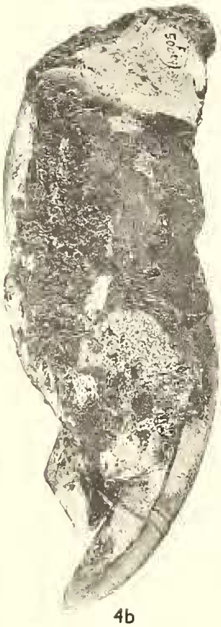


4a



4b

STEPHENSON, *Diarcodon parvus*